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Senescent changes in scotopic contrast sensitivity

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Abstract

Scotopic contrast sensitivity functions (CSFs) were measured for 50 observers between the ages of 20 and 88 years. Using a maximum-likelihood, 2-alternative, temporal forced-choice threshold-estimation algorithm, scotopic CSFs were measured at 7 spatial frequencies ranging from 0.2 to 3.0 cpd, with mean retinal illuminance equated for observers at -0.85 log scotopic Trolands. For each stimulus condition, eight cycles of a horizontal sinusoidal grating were presented within ± 1 S.D. of a 2-D Gaussian-spatial envelope and within a 1-s Gaussian-temporal envelope. Stimuli were centered on the nasal retina along the horizontal meridian 6° from the fovea. Scotopic CSFs were found to be low-pass. Statistically significant age-related declines in contrast sensitivities were found for spatial frequencies at or below 1.2 cpd. There was also a statistically significant decrease in the high frequency cut-off with age ($P < 0.01$). An explanation of these results in terms of optical factors is rejected, while the results are consistent with age-related changes in the magnocellular pathway.

Keywords: Aging; Scotopic vision; Contrast sensitivity function; Scotopic contrast sensitivity

1. Introduction

Human psychophysical studies and electrophysiological recordings obtained from monkey and cat provide strong support for the idea that spatial vision is subserved by multiple mechanisms that are tuned to narrow bands of spatial frequency (DeValois & DeValois, 1988). Contrast sensitivity functions have been used to characterize the combined ability of these putative spatial mechanisms to mediate detection of sinusoidal luminance modulation about an ambient light level. Under photopic conditions, there appears to be a gradual change in the shapes of these functions across the life span. Results from studies in which contrast sensitivity functions have been measured in subjects free from ocular disease and refracted for the test distance agree with one another in showing that age-related losses in sensitivity are greater for high than middle and low spatial frequencies (Owsley, Sekuler & Siemsen, 1983; Higgins, Jaffe, Caruso & deMonasterio, 1988; Tulunay-Keesey, Ver Hoeve & Terkla-McGrane, 1988). Furthermore, because these studies found small, if any, differences in contrast sensitivity to frequencies ≤ 1 cpd, it is questionable whether there are age-related losses at these low spatial frequencies.

Under photopic conditions, both senescent changes in the optical properties of the eye (Artal, Ferro, Miranda & Navarro, 1993; Burton, Owsley & Sloane, 1993) and neural mechanisms responsible for processing spatial information (Morrison & McGrath, 1985; Sloane, Owsley & Jackson, 1988; Nameda, Kawara & Ohzu, 1989) are thought to underlie the age-related deterioration of contrast sensitivity at high spatial frequencies, whereas neural factors would appear to play a more prominent role in the explanation of possible age-related declines in sensitivity to spatial frequencies below approximately 2 cpd. Sloane et al. (1988) found that differences in detection thresholds for a 0.5 cpd test grating between younger and older observers increased as the mean luminance of the stimulus shifted from photopic to mesopic light levels. This result raises the intriguing possibility that senescent changes in rod pathways may lead to age-related losses in contrast sensitivity to low spatial frequencies under scotopic conditions. Consistent with this notion is an analysis by Schefrin, Bieber, McLean and Werner (1998) indicating

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that neural changes, perhaps notable losses in rods (Curcio, Milican, Allen & Kalina, 1993) and ganglion cells (Curcio & Drucker, 1993) within the central retina, rather than senescent changes in the eye's optics must be invoked to account for age-related enlargements of the area of complete spatial summation (Ricco's area) under scotopic conditions. It is not clear from this spatial summation study whether age-related changes in performance are due to specific spatially-tuned mechanisms or to an overall reduction in scotopic contrast sensitivity. For this reason, we have measured contrast sensitivity functions under scotopic conditions across adulthood.

2. Methods

2.1. Subjects

Fifty subjects (25 male and 25 female) ranging in age from 20 to 88 years participated in this experiment. At the time of testing, subjects reported that they were free from ocular disease and they neither had any systemic complications nor were they taking medications known to interfere with normal visual functioning. All subjects were normal trichromats according to the Neitz anomaloscope, Farnsworth Panel D-15 test, F-2 plate, and AO HRR pseudoisochromatic plates. Based upon an undilated ophthalmoscopic evaluation of the optic nerve head, retina, and retinal vasculature, all subjects appeared free from retinal disease. Forty-five of the 50 subjects possessed clear ocular media, and five subjects demonstrated a few scattered punctate lenticular opacities. These latter five subjects were included in the study because their visual acuities were either equal to or better than the appropriate age-related mean acuity reported by Owsley et al., (1983). Best-corrected distance acuities were measured on all subjects using the Bailey Lovie Log MAR Chart #4. Acuities ranged from 20/15 to 20/35 for all subjects. All but two subjects under the age of 64 years had best corrected distance visual acuities of 20/25 or better. The visual acuity was better than 20/30 for the remaining two subjects. Of the thirteen subjects older than 64 years, four of them had Snellen acuities that ranged from 20/30 to 20/35. These visual acuities are equivalent to or better than subjects of comparable age who have served in studies of photopic spatial vision (e.g. Owsley et al., 1983). In addition, essentially the same regression parameters and significance levels were obtained when statistical analyses were repeated without these subjects.

Prior to any testing, all subjects provided written informed consent. Our experimental protocol was in accord with the tenets of the Declaration of Helsinki and was reviewed by the Human Research Committee at the University of Colorado at Boulder.

2.2. Apparatus and stimuli

The stimuli were horizontally oriented sinusoidal gratings presented within a 2-D Gaussian-spatial envelope in sine phase so that the luminance distribution followed the equation:

$$f(x, y) = L_0 \cdot m \cdot \sin(b \cdot y) \cdot \exp\{-[(x/s)^2 + (y/s)^2]\} + L_0.$$

Here L_0 is the mean luminance, m is the amplitude, and s is the standard deviation of the Gaussian ($=1$/spatial frequency). The standard deviations were equal in the x and y directions. The number of cycles was held constant at eight (at ± 1 S.D.) in view of evidence that contrast thresholds for sinusoidal gratings are influenced by the number of cycles presented in the stimulus under both photopic and scotopic conditions (Howell & Hess, 1978; Savage & Banks, 1992). To limit the representation of our stimuli within the temporal frequency domain, the Gabor patches were presented with a 1 s Gaussian temporal envelope such that maximal contrast was attained 0.5 s from the start of the trial.

These stimuli were displayed on a three-color high-resolution computer monitor (Apple Multiple Scan 1705 display) controlled by a Power Macintosh (8600/200). The three phosphors were combined by a CVS SR video attenuator (Pelli & Zhang, 1991) to produce a luminance-varying signal with a minimum of 12-bit level resolution. This signal drove the green phosphor of the monitor (dominant wavelength 548 nm; 80 nm bandwidth at half power) and produced a maximum Michaelson contrast of 86%.

A spectroradiometer/photometer (Photo Research, Model PR703-A) was used to measure the radiometric output of the monitor in 2 nm steps. The retinal illuminance was then calculated for hypothetical 20- and 80-year-old observers by convolving the radiometric data with the scotopic luminosity function (Wyszecki & Stiles, 1982). The latter functions were assumed to differ for our hypothetical observers due to age-related changes in ocular media density, which were assumed to follow an equation by Werner (1982) that describes average ocular media density as a function of age at 400 nm. Densities at other wavelengths were obtained by multliplicative scaling of a standard ocular media density spectrum tabled by Norren and Vos (1974). An equal pupil area for each hypothetical observer was assumed due to the use of an artificial pupil that was smaller than the pupillary area of observers at both ages (see below for further justification of this assumption). From these calculations, the difference in retinal illuminance between the average younger and older observers amounted to only 0.1 log scotopic Troland.

A two-channel Maxwellian-view optical system was used to combine the stimuli from the monitor and a

fixation point, while controlling for age-related variations in pupil diameter. In channel 1, subjects viewed the stimuli at optical infinity through a 6 × astronomical telescope. A 15 mm field stop was placed before the telescope so that its 2.5 mm diameter image formed the exit pupil of this optical system and was coincident with the center of the subject's natural pupil. Subjects were aligned with the exit pupil using a chin rest and forehead restraint. A review of the literature indicates that an exit pupil of this size is smaller than natural pupils for individuals across the age range of our subjects under our experimental conditions (Loewenfeld, 1979). Thus, the effective pupil area was constant across subjects. A second channel was used to form a fixation point from a red LED so that the sinusoidal gratings were centered along the horizontal meridian at 6° nasal eccentricity. The luminance of the monitor was controlled by interposing calibrated neutral density filters between the monitor and the telescope. The mean retinal illuminance was essentially equated at −0.85 log scotopic Trolands for all subjects.

2.3. Procedure

Subjects dark adapted for 30 min prior to testing. At each tested spatial frequency, they would then light adapt for 1 min to a blank screen of the same space average luminance as the test gratings. Contrast thresholds were measured at seven spatial frequencies (0.2, 0.4, 0.8, 1.2, 1.8, 2.4, and 3.0 cpd) using a maximum-likelihood (Harvey, 1986, 1997), 2-alternative, temporal forced-choice procedure. For each spatial frequency, the threshold stimulus contrast corresponded to a detection probability of 75%, based on a logistic psychometric function.

3. Results

Initially, contrast sensitivity data for all observers were best fit with a linear function when the data were plotted in log–linear coordinates, i.e. log contrast sensitivity as a function of spatial frequency. (We found that more elaborate functions did not significantly improve the fit to our data.) Fig. 1 shows contrast sensitivity functions, plotted in log–log coordinates, for four observers who approximately span the age range of our sample. The symbols represent log contrast sensitivity and the error bars represent the 95% confidence limits of the sensitivity estimate. The curve in each panel represents the aforementioned function best fit to each data set. The data shown in the four panels are repre-

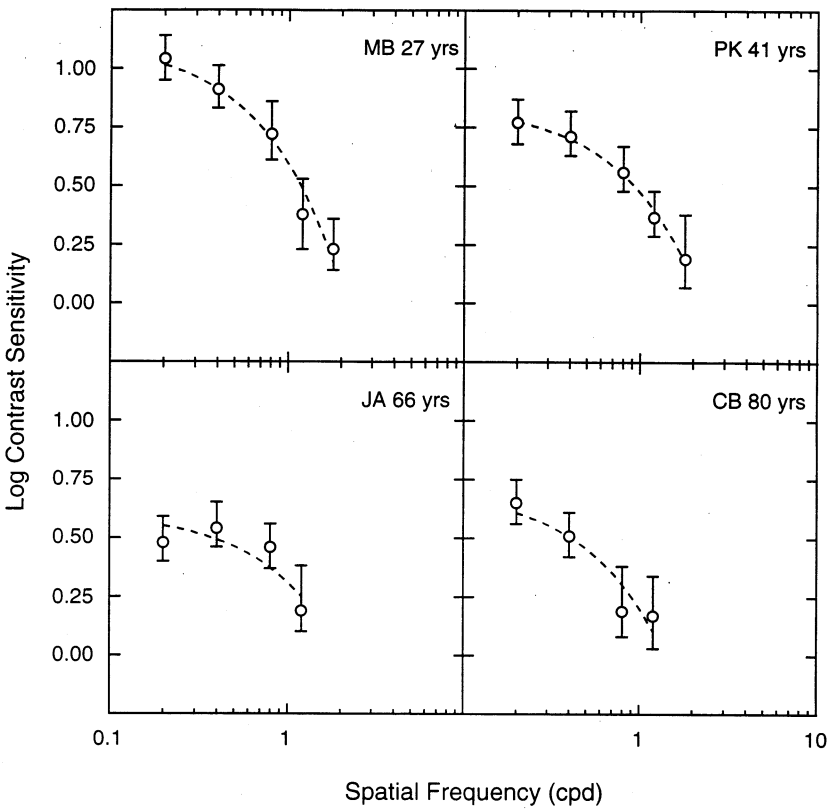

Fig. 1. Log contrast sensitivity for four observers plotted as a function of spatial frequency. Symbols and error bars represent contrast sensitivity and the 95% confidence limits of the sensitivity estimate, respectively. The dashed curve passing through each data set represents the best-fitting linear function.

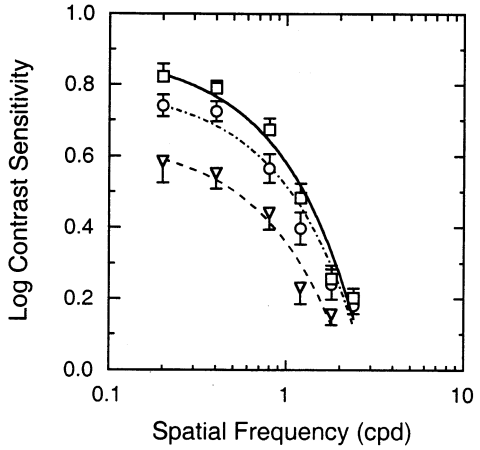

Fig. 2. Average contrast sensitivity for three age groups plotted as a function of spatial frequency. The squares, circles, and triangles represent average sensitivities for subjects aged 20–40, 41–60, and 61–88 years, respectively. Error bars represent 1 S.E. of the mean.

sentative of data sets obtained from observers of approximately the same age. Consistent with previous studies (Daitch & Green, 1969; D'Zmura & Lennie, 1986; Savage & Banks, 1992), the shapes of individual scotopic contrast sensitivity functions for all observers appeared to be low-pass (cf. Fiorentini & Maffei, 1973).

Fig. 2 shows average scotopic contrast sensitivity functions for three arbitrarily arranged age groups. The squares, circles, and triangles represent average log contrast sensitivities for 20–40, 41–60, and 61–88 year old subjects, respectively. Error bars represent 1 S.E. of the mean. (For the sake of clarity, only the positive and negative error bars are shown for the 20–40 and 61–88 year old age groups, respectively.) This figure suggests an age-related decline in contrast sensitivity across all spatial frequencies.

Fig. 3 presents data for all subjects plotted in terms of log contrast sensitivity as a function of age. Separate panels show each of the tested spatial frequencies except for the 3.0 cpd condition. These latter data are not shown because only three of our 50 subjects were able to detect it at the maximal contrast of our monitor. The spatial frequency of each stimulus is given in the upper right-hand corner of each panel. The straight line in each panel represents the linear regression fit to each set of data. Descriptive statistics for the samples and parameters for the least-squares linear regression equations are summarized in Table 1. As can be seen in the table, the slopes of the regression lines fitted to the four lowest spatial frequencies (0.2–1.2 cpd) are similar and the regression analyses indicate a statistically significant loss in contrast sensitivity in each case. The slopes of the regression lines for the two highest spatial frequencies (1.8 and 2.4 cpd), which are virtually identical to each other, show that contrast sensitivity declines at a slightly slower rate of 0.020 log unit per decade. These latter changes in sensitivity are not, however, significantly different from zero.

The data reveal two bands of spatial frequencies with different rates of age-related loss in scotopic contrast sensitivity, ≤ 1.2 cpd and > 1.2 cpd. Unfortunately, there are potential floor effects for the higher spatial frequency band because it is outside the cut-off frequency of some subjects. This issue was addressed by an analysis of covariance taking into account covariate interactions (Judd, McClelland & Smith, 1996). This analysis was conducted using only those subjects for whom we had complete data sets ($n = 37$) for spatial frequencies from 0.2 to 1.8 cpd. The results indicated that the slopes of the regression lines for the four lowest spatial frequencies are not significantly different from each other, but significantly different from the slope of the regression line fit to the 1.8 cpd data ($F_{1,35} = 3.93$, $P = 0.05$, $r = 0.32$). As with the aforementioned regression analyses, these analyses demonstrate that the rates of decline in contrast sensitivity across the life span are greater for spatial frequencies ≤ 1.2 cpd than for the 1.8 cpd data.

Fig. 4 shows the change in the high spatial frequency cut-off for individual observers plotted as a function of age. These values correspond to the point where the linear function best fit to each subject's data (in log–linear coordinates) intersected the spatial frequency axis (see Fig. 1). Consistent with the results in Figs. 2 and 3 there is a significant age-related decline in the high spatial frequency cut-off (see Table 1 for details).

The suggestion from the scattergrams presented in Figs. 3 and 4 is that the changes in scotopic contrast sensitivity can be adequately described by a linear relation with age. This is different from the models suggested by photopic contrast sensitivity studies, although the age at which declines in photopic contrast sensitivity are first measurable depends upon the spatial and temporal frequency characteristics of the gratings (Tulunay-Keesey et al., 1988). Age-related losses in contrast sensitivity to sinusoidal gratings of low-to-middle spatial and temporal frequency (below approximately 5 cpd and 5 Hz) are not evident until the fifth decade of life (Derefeldt, Lennerstrand & Lundh, 1979; Owsley et al., 1983; Tulunay-Keesey et al., 1988; Nameda et al., 1989). To determine whether a similar pattern of sensitivity loss as a function of age could describe our data, we compared the fits of linear and bilinear functions to the data sets shown in Fig. 3 using a least-squared error criterion. Three separate bilinear functions were fit to each data set. For each fit the value of the inflection point of the bilinear function was constrained to be 35, 45, or 55 years of age, whereas the slopes of the two limbs of the function were allowed to vary freely. The values of the inflection points were somewhat arbitrarily chosen to span the age range over

which age-related losses in contrast sensitivity are first observed for low spatial frequencies. In every case, the bilinear model could not account for a significantly greater amount of the variance in contrast sensitivity measured across the age range of our sample when compared to the linear regression model ($F_{2,n-4}$; $P > 0.05$).

3.1. Control experiment-potential effects of dark focus myopia on age-related changes in scotopic contrast sensitivity

Under mesopic and scotopic conditions, optical defocus has been shown to decrease contrast sensitivity at low spatial frequencies (Bedell, 1987; Coletta & Maggisano, 1998). In this experiment, measures of scotopic contrast sensitivity were obtained from subjects without the use of a cycloplegic agent. It is possible, therefore, that their contrast sensitivities were reduced secondary to dark focus myopia which has been reported to produce an average of 1.7 D of positive defocus in a large group of young observers (Leibowitz & Owens, 1986).

To evaluate the effects that myopic defocus may have on contrast sensitivity under our experimental conditions, contrast thresholds were measured with three subjects ranging in age from 19 to 43 years, with and without 2D of positive defocus. To maintain a constant state of accommodation for each observer, one drop of a cycloplegic agent (1% tropicamide) was instilled into the test eye 30 min prior to testing. Contrast thresholds were measured for a subset of spatial frequencies (0.4, 1.8, 2.4 cpd) used in the main experiment and then repeated under conditions of myopic defocus by placing a +2 D lens in front of the subject's eye. The results from all three observers showed that 2D of myopic defocus produced no change in sensitivity at 0.4 cpd and average losses of 0.06, and 0.16 log unit in contrast

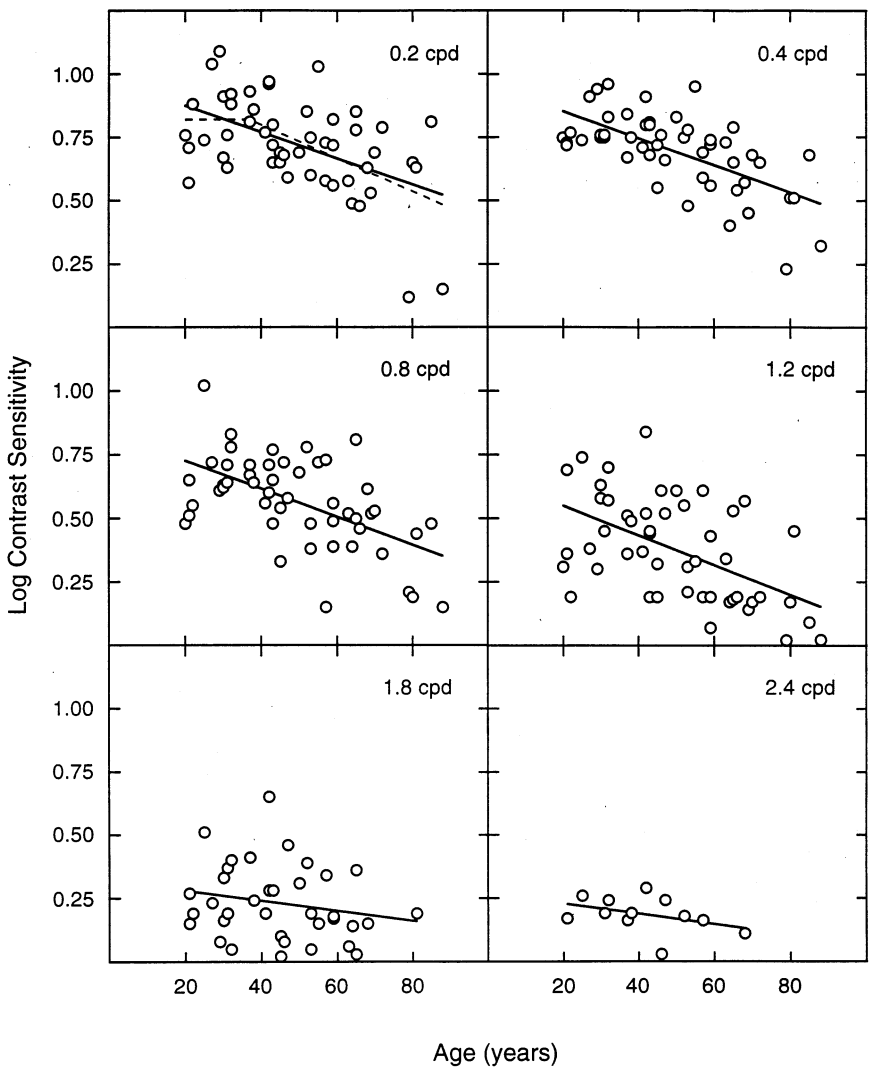

Fig. 3. Log contrast sensitivity of individual observers plotted as a function of age for spatial frequencies indicated within each panel. The line passing through each data set represents a linear function best fit to the data.

Table 1
Descriptive statistics and parameters of linear regression as a function of age for contrast sensitivity

Spatial frequency (cpd)	Slope	Intercept	r	F	n
0.2	−0.0053	0.96	0.64	32.95[a]	50
0.4	−0.0053	0.96	0.64	32.95[a]	50
0.8	−0.0055	0.84	0.56	22.17[a]	50
1.2	−0.0058	0.67	0.53	18.78[a]	50
1.8	−0.0025	0.34	0.25	2.43	37
2.4	−0.0021	0.27	0.40	1.89	12
High spatial frequency cut off	−0.0166	3.20	0.50	16.28[a]	50

[a] $P<0.05$

sensitivity at 1.8 and 2.4 cpd, respectively. These results are consistent with data from other studies obtained under photopic and mesopic conditions indicating that small diameter pupils, such as the 2.5 mm effective pupil diameter used in this study, help to maintain contrast sensitivity to low spatial frequencies that would otherwise decline in response to the introduction of ocular aberrations and optical defocus (Green & Campbell, 1965; Charman, 1979; Coletta & Sharma, 1994). Thus, it appears unlikely that differences in the average contrast sensitivity functions below approximately 1.2 cpd for the three age-groups shown in Fig. 2 are due to potential age-related differences in dark focus. Previous studies have demonstrated a decline in the magnitude of dark focus with age (Simonelli, 1983; Ramsdale & Charman, 1989). If anything, the deleterious effects of dark focus myopia should produce relatively greater losses in sensitivity in younger than older observers thereby lessening the age-related changes in contrast sensitivity reported in this paper.

4. Discussion

The results of this study show an overall age-related loss in scotopic contrast sensitivity with significant losses occurring for spatial frequencies ≤ 1.2 cpd. We are not aware of any previous aging studies with which to compare these results, but there are data in the literature with which to compare our high spatial frequency cut-offs. Because the high spatial frequency cut-off is lowered with decreases in the space-average retinal illuminance of the gratings (Daitch & Green, 1969; Hess, Nordby & Pointer, 1987) and increases in age, one must take these two factors into account along with the retinal location of the stimulus when drawing comparisons between studies. Stimuli for our study and that of Savage and Banks (1992) were centered along the horizontal meridian in the nasal retina at 6 and 20° retinal eccentricity, respectively. For the retinal illuminance of −0.85 log scotopic Trolands used in this study, we estimate that the high spatial frequency cut-off would be about 1 cpd for the two subjects (approximately 40 years of age) participating in the study of Savage and Banks. For our subjects of comparable age, the cut-off frequency is about 2.5 cpd (see Fig. 4). In contrast, Lennie and Fairchild (1994) reported cut-offs of about 5 cpd from about 5 to 20° temporal retinal eccentricity for stimuli with a space-average luminance of −0.44 log scotopic Trolands. While differences between these estimates of the high spatial frequency cut-off may seem minor, it should be remembered that only three of our 50 subjects could detect a 3 cpd grating. It is doubtful that differences in mean retinal illuminance levels and retinal location of the stimuli between these studies can account entirely for the range of estimated cut-off frequencies. At a mean retinal illuminance level that is approximately 1.2 log units *higher* than the level used by Lennie and Fairchild, the estimated cut-off frequencies for subjects in the study of Savage and Banks is at most 3 cpd. Furthermore, anatomical results from human (Curcio & Allen, 1990) and macaque (Perry, Oehler & Cowey, 1984) retina indicate greater ganglion cell densities are found in the nasal rather than temporal retina. The Nyquist limit should, therefore, be higher in the nasal compared to the temporal retina at equivalent eccentricities. It is also

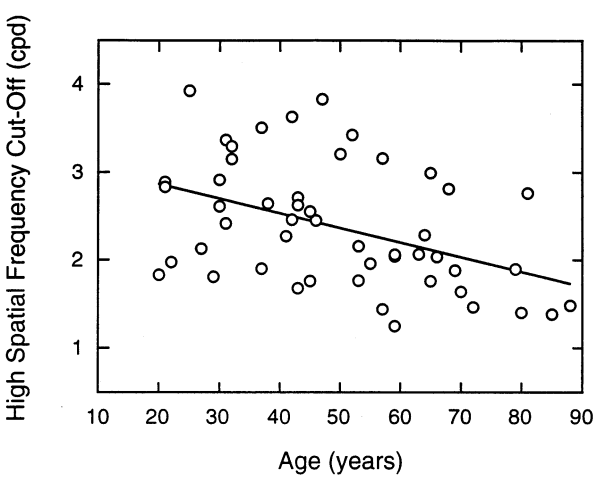

Fig. 4. High spatial frequency cut-off of individual observers plotted as a function of age. The solid line was fitted to the data using a least-squares linear regression.

unlikely that the higher cut-off values reported by Lennie and Fairchild could be explained by the fact that, unlike the other two compared studies, the contrast of their gratings was temporally modulated at 4 Hz when presented within a Gaussian temporal envelope. Although it appears to be the case that contrast sensitivity to low spatial frequency gratings is enhanced when the contrast of the grating is modulated at a low-to-moderate temporal frequency under photopic conditions (Kelly, 1977), this same combination of parameters fails to enhance contrast sensitivity measured under scotopic light levels (Hess et al., 1987). It is presently unclear to us why our study and the studies cited above differ in their estimates of the high spatial frequency cut off obtained under scotopic conditions.

The senescent changes in scotopic contrast sensitivity demonstrated in this study are likely to be due primarily to neural rather than optical factors. Perhaps the most plausible explanation of our results involving optical factors comes from interpretations by Bedell (1987), Coletta and Maggisano (1998), Coletta, Maggisano and Hersey (1998), of their data, showing that even when pupil size is kept constant across luminance levels, the deleterious effects of positive defocus on contrast sensitivity at low spatial frequencies increase as the space-average luminance of the stimulus decreases from photopic to scotopic levels. These authors and others (e.g. Green & Campbell, 1965) suggest that optical aberrations of the eye are partially responsible for lowering contrast sensitivity at scotopic luminance levels due to a lessening of the Stiles-Crawford effect. Since the Stiles-Crawford effect reduces the effective pupil size to a greater extent under photopic as compared to scotopic conditions, aberrations of the eye and defocus could have a larger effect on image quality at low ambient light levels. Consistent with this argument are data demonstrating declines in the efficiency of the eye's optical transfer function occurring with increases in pupillary diameter (Campbell & Gubisch 1966), as would occur at scotopic light levels, or with increasing age (Artal et al., 1993; Liang & Westheimer, 1995).

It is, however, unlikely that the significant age-related losses in contrast sensitivity to spatial frequencies ≤ 1.2 cpd can be explained entirely by the types of preneural factors discussed above. Previously, Schefrin et al. (1998) modeled optical transfer functions at 6° nasal eccentricity for hypothetical 30- and 65-year-old observers (the open diamonds and closed circles, respectively, in their Fig. 4). Based upon a comparison of these functions, one would predict that preneural factors would account for at most a 0.04 log unit loss in contrast sensitivity to spatial frequencies ≤ 1 cpd. The loss in sensitivity over these same spatial frequencies and age range is predicted to be approximately 0.2 log unit based on the linear regressions fit to the data shown in Fig. 3. It is doubtful that under our experimental conditions the remaining loss in sensitivity can be explained by a diminished Stiles-Crawford effect especially if one considers that for relatively small pupils there is little difference between the shapes of the Stiles-Crawford function under photopic and scotopic light levels (Crawford, 1972). As mentioned earlier, small pupil diameters, similar to the effective pupil size used in this experiment, tend to vitiate the deleterious effects of optical aberrations upon contrast sensitivity over the range of spatial frequencies used in this study. Indeed, even at photopic light levels, only negligible age-related changes in sensitivity to low spatial frequencies have been reported for studies using either natural or artificial pupils (Owsley et al., 1983; Higgins et al., 1988; Tulunay-Keesey et al., 1988).

At first glance, it is difficult to ascertain whether the differential aging effects in contrast sensitivity for spatial frequencies above or below 1.2 cpd are due to changes in one or more spatial filters or to a floor effect. The problem of a floor effect at high spatial frequencies is not unique to this study, but inherent in any study of contrast sensitivity due to individual differences in the high spatial frequency cut-off. Note, however, that the differential loss in contrast sensitivity above or below 1.2 cpd is evident whether statistical analyses include data from all subjects or are confined to those subjects having complete data sets below 2.4 cpd. Moreover, the differential losses over two bands of spatial frequencies are consistent with other studies (Greenlee, Magnussen & Nordby, 1988; Hess and Howell 1988) indicating that more than one spatial mechanism mediates the detection of sinusoidal gratings under mesopic and scotopic conditions similar to those used in this study. Thus it is possible that different spatial mechanisms undergo senescence at different rates and that one mechanism that is sensitive to low spatial frequencies loses sensitivity more rapidly with age than other mechanisms tuned to relatively higher spatial frequencies. This interpretation is supported by the results shown in Fig. 3 revealing similar rates of decline in contrast sensitivity with age for spatial frequencies ≤ 1.2 cpd, and the work of Greenlee et al. suggesting that for trichromats there is only a single spatial mechanism mediating detection of test gratings below 1 cpd.

What is the neuronal basis for age-related losses in sensitivity of a mechanism tuned to low spatial frequencies? One possibility is that there are age-related changes in the magnocellular pathway. Anatomical (Grunert, 1997), physiological (Purpura, Kaplan & Shapley, 1988; Lee, Smith, Pokorny & Kremers, 1997), and psychophysical evidence (D'Zmura & Lennie, 1986; Lennie & Fairchild, 1994) indicate that rod signals pass through ganglion cells that project to both the parvocellular (P-cells) and magnocellular (M-cells) layers of the lateral geniculate nucleus (LGN). Purpura et al.

(1988) measured the contrast gain (impulses/s/% contrast) of P-cells and M-cells of the macaque LGN over a broad range of retinal illuminances. Most pertinent to our proposal is their finding that under their experimental conditions the contrast gain of M-cells could still be measured at retinal illuminances corresponding to 0 log scotopic Trolands in humans whereas the gain of P-cells could not be measured below a retinal illuminance level corresponding to 0.1 log scotopic Trolands. The space-average retinal illuminance in our study was approximately 1 log unit less than the lowest level investigated by Purpura et al. so their results suggest that for the low scotopic light levels used in our study, threshold detection of luminance contrast is mediated by magnocellular pathways.

A second factor that leads us to suggest that age-related changes in magnocellular pathways underlie our results is that the high spatial frequency cut-off for our observers approximates the Nyquist limit that is predicted by assuming that the stimulus is sampled by a regular hexagonal array of ganglion cells that project to M-cells in the LGN. Lennie and Fairchild (1994) calculated Nyquist limits as a function of retinal eccentricity for the magnocellular pathway. In their calculations they used the total number of ganglion cells reported by Curcio and Allen (1990) and made the following two important assumptions: each sampling element in the array consists of a pair of ON-center and OFF-center ganglion cells, and that out of the total number of ganglion cells the *proportion* of cells projecting to the magnocellular layers, reported by Silveira and Perry (1991), is the same in macaque and human. Following their approach, with the exception that we used ganglion cell field densities (from Curcio, 1996) which take into account ganglion cell bodies displaced from the fovea, we calculated the Nyquist limits for hypothetical younger (33.7 years) and older (70.5 years) observers using the following equation:

$$\text{Nyquist limit (cpd)} = (d^{-1})\ (3^{-0.5}).$$

Here d represents the angular separation (286 μm = 1°) between sampling elements. At 6° nasal eccentricity the calculated Nyquist limits for our younger and older observer are 4.0 and 3.3 cpd, respectively, for their M-cell mosaic. These values are slightly higher than the high spatial frequency cut-offs estimated from our data (see Fig. 4) implying that for our experimental conditions, we cannot reject the hypothesis that detection of the gratings was mediated by the magnocellular pathway.

Age-related changes in the contrast gain of cells comprising a portion of the magnocellular pathway might account for the generalized decline in scotopic contrast sensitivity. Consistent with this notion are results showing that the rate of change in contrast sensitivity to low spatial frequencies differs between younger and older observers over a range of mesopic to photopic luminance levels (Sloane et al., 1988).

The present study thus shows an age-related loss in scotopic contrast sensitivity for spatial frequencies ≤ 1.2 cpd. The rate of decline in sensitivity across the life span is essentially the same for all tested spatial frequencies between 0.2 and 1.2 cpd. It is possible that age-related changes in the contrast gain of a single spatial mechanism can account for these data, and we speculate that they take place within the magnocellular pathway.

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